

THE *GONOLOBUS* COMPLEX (APOCYNACEAE:  
ASCLEPIADOIDEAE) IN THE  
SOUTHEASTERN UNITED STATES

Alexander Krings

Herbarium, Department of Botany  
North Carolina State University  
Raleigh, North Carolina 27695-7612  
Alexander\_Krings@ncsu.edu

(Jenny) Qiu-yun Xiang

Department of Botany  
North Carolina State University  
Raleigh, North Carolina 27695-7612  
Jenny\_Xiang@ncsu.edu

ABSTRACT

Taxonomic limits of *Gonolobus* (Apocynaceae: Asclepiadoideae) in the southeastern United States have been controversial, with some authors recognizing two species and others only one. Over the past 30 years, most authors have tended toward recognition of a single species. However, the morphological variation within the taxon appears complicated and has not been analyzed using a quantitative approach. We analyzed the morphological variation within southeastern *Gonolobus*, based on 143 herbarium specimens from 13 southeastern states, using ANOVA, and mapped taxon distributions. Two distinct *Gonolobus* entities, based on differences in floral character states and geographic tendencies, appear to exist in the southeast, although questions regarding rank recognition remain.

RESUMEN

Los límites taxonómicos de *Gonolobus* (Apocynaceae: Asclepiadoideae) en el sureste de los Estados Unidos han sido controvertidos, con unos autores que reconocen dos especies y otros sólo una. En los últimos 30 años, la mayoría de los autores han tendido al reconocimiento de una sola especie. Sin embargo, la variación morfológica del taxon parece complicada y no ha sido analizada usando métodos cuantitativos. Hemos analizado la variación morfológica en los *Gonolobus* del sureste, en base a 143 especímenes de herbario de 13 estados del sureste, usando ANOVA, y distribuciones cartográficas del taxon. En el sureste parecen existir dos entidades distintas de *Gonolobus*, basadas en diferencias de los estados de carácter florales y las tendencias geográficas, aunque aún quedan cuestiones acerca del rango que merecen.

Climbing milkweeds (Apocynaceae: Asclepiadoideae and Periplocoideae) encompass at least two taxonomically difficult genera in the southeastern United States—*Matelea* and *Gonolobus* (Drapalik 1969; Sundell 1981; Rosatti 1989; Liede 1997). Two closely-related species of *Gonolobus* Michx. have until recently been recognized from the southeastern United States, although opinions over generic placement have differed. Woodson (1941) considered that the genus *Gonolobus* should contain plants characterized by only long, eglandular trichomes, dorsal anther appendages, and smooth, angled or winged foliicles, whereas *Matelea* Aubl. should contain plants characterized by glandular and eglandular trichomes, anthers lacking dorsal appendages, and muricate foliicles. Unconvinced that dorsal anther appendages should serve as a generic character and citing examples of smooth [but not angled or winged] fruits in *Matelea*, Shinnors (1950) argued against Woodson's generic concept and transferred the southeastern

*Gonolobus* taxa to *Matelea*. Later, Shinnery (1964) also included twelve of Woodson's (1941) *Gonolobus* combinations in *Matelea*. Drapalik (1969) maintained Shinnery's generic view, although admitting to the characteristic differences of southeastern *Gonolobus* from southeastern *Matelea* species in bearing dorsal anther appendages and smooth, winged follicles. Taking a broader geographical perspective of generic morphology and citing the importance and development of anther appendages in the 150 some species of *Gonolobus* outside the southeastern United States, Rosatti (1989) argued for renewed placement of the southeastern taxon in *Gonolobus*. Most recently the concept of *Gonolobus* as characterized by short, capitate-glandular, short acicular, and long acicular trichomes, dorsal anther appendages (typically), and smooth, winged follicles has been used by Stevens (2001). The two *Gonolobus* species historically recognized from the southeastern United States—*Gonolobus suberosus* (L.) R. Br. and *Gonolobus gonocarpus*—have been distinguished primarily by the ratio of corolla lobe length to sepal lobe length and the presence or absence of pubescence on the adaxial corolla surface (Small 1933; Perry 1938; Fernald 1950; Gleason 1952; Radford et al. 1968). Most authors essentially followed Small (1933) in referring the taxon with glabrous corollas and lobes more than twice as long as the sepals to *G. gonocarpus* and the taxon with pubescent corollas and lobes twice as long or less than the sepals to *G. suberosus* (Perry 1938; Fernald 1950; Gleason 1952; Radford et al. 1968). In contrast, Drapalik (1969) considered the two taxa synonymous, having found "plants that would represent both [...] taxa and every conceivable intermediate." However, he stressed that in no manner should his decision be taken to acknowledge that the taxon was uniform throughout its range. Considering that *G. gonocarpus* is state listed as threatened in Florida (Florida Administrative Code Ch. 5B- 40.0055), this study seeks to re-examine the taxonomy of the southeastern *Gonolobus* complex by critically analyzing patterns of morphological variation and their geographical relationships using a quantitative approach.

#### METHODS

A total of 326 herbarium specimens (from nineteen herbaria) were examined from throughout the range of the southeastern *Gonolobus* complex (i.e., AL, AR, FL, GA, KY, LA, MS, NC, OK, SC, TN, TX, and VA). We selected 143 herbarium specimens (the OTUs in the analysis) for our analyses—the rest were either too poor in condition or lacked some or all organs. Six characters (Table 1), three quantitative and three qualitative, showed variation within the group and were thus chosen for the analysis. Only mature flowers were chosen for scoring of floral characters.

Leaf shape/size and vestiture characters were not chosen for inclusion in the analysis. These characters were not rejected due to high variability, but due to lack of basic understanding regarding intra-individual variation. Leaf size

and shape may be influenced by position on the stem (e.g., sun vs. shade leaves) and habitat (e.g., edge vs. forest interior) (Krings, pers. obs.). As collectors rarely indicate the stem position from which samples were taken, parallel comparisons of herbarium specimen leaf material (i.e., comparing sun leaves to sun leaves) is essentially impossible. Leaf pubescence characteristics were also considered uninformative with regard to southeastern *Gonolobus*. Our chi-square tests suggested no correlation between leaf pubescence and either floral character states or the environment (i.e., habitat), as might be expected (unpubl.).

Although inflorescence characters (type and number of flowers borne) have been useful in higher level analyses in the Asclepiadoideae (e.g., Liede 1996, 1997), inflorescence characters were not included in our study based on results of a preliminary analysis of 48 *Gonolobus* specimens chosen primarily from the extremes of the range (i.e., Florida and Texas). ANOVA results showed no significant difference ( $F=0.865 < F_{\text{crit}}=4.05$ ) in the mean number of flowers per inflorescence between uniformly-colored and multi-colored specimens (Krings, unpubl.). In the preliminary analysis, flowers were counted for any inflorescence bearing at least one fully opened flower (i.e., corolla lobes completely extended). As flowers are produced sequentially over the life of the inflorescence, visible flower buds were included in the total count of flowers per inflorescence. Specimens chosen for inclusion were those most robust overall—a somewhat arbitrary judgment of the number of inflorescences available and their condition.

Due to the high similarity of fruits of *Gonolobus* in the southeast, collections of the same individuals in flower and fruit would be required to allow correlative evaluation of fruit character utility. Unfortunately, the extremely small number of such collections is inadequate for such an evaluation at this time.

A data matrix was produced by scoring the character states of five characters for all 143 OTUs (see below & Table 1). There were no gaps in the data matrix. A neighbor-joining tree was generated using PAUP 4.0 (Swofford 2002). Frequency distributions were also determined for selected floral character states and tested for significant differences using ANOVA.

### Characters

1. *Floral color*.—Individuals of the southeastern *Gonolobus* complex exhibit flowers that are either uniformly green from corolla lobe base to apex or conspicuously dark at the base (variously described as maroon to brown) with lighter tips (typically green). Specimens bearing the former were scored as uniformly green (1) and specimens exhibiting the latter as multi-colored (0) for corolla lobe coloration. On senescing, greenish flowers tend to turn yellowish.

2. *Adaxial corolla vestiture*.—Adaxial corolla vestiture is an important character that has been used to recognize species in the southeastern *Gonolobus* com-

plex (see Small 1933; Gleason 1952; Radford et al. 1968). Adaxial corolla lobe pubescence tends to be laterally distributed. Pubescence is generally concentrated on the right side of corolla lobes (from apex to base) and may extend longitudinally to various degrees across the lobe center to the left. The far left margins (from apex to base) tend to be glabrous in otherwise pubescent flowers. The same asymmetry was also evident in Caribbean species available to us for inspection and may be the case for all pubescent *Gonolobus* species—although such analysis was presently beyond our scope. Specimens were scored as pubescent (0) if pubescence to any degree was observed on the adaxial corolla lobes and glabrous (1) if no pubescence was evident.

3. *Corona*.—Corona characters have in the past been used to distinguish asclepiad genera (see Liede 1996), although caution must be employed if the true homology is not known (see Liede 1996; Liede & Täuber 2002). In our study, we evaluated only the shape of the corona lobes among members of the southeastern *Gonolobus* complex. All coronas in the complex are lobed. However, not all lobes are further lobed (i.e., emarginate at the apex). We scored corona lobes to be either lobed (i.e., emarginate at the apex)(0) or truncate (i.e., squared off at the apex)(1).

4–6. *Quantitative floral characters*.—Measurements of sepal and petal length were taken from between 1 to 5 flowers per specimen, depending on availability and measurability. Flowers with excessive contortion and folding of petals and sepals were avoided. In general, measurements were taken from different flowers, although in a few cases, when availability was poor and lobe length varied infrapleurally, multiple corolla lobes were measured from a single flower. For generation of a nearest-neighbor tree, continuous sepal and corolla lobe lengths were coded into one of five range classes and treated as unordered in the analysis (Table 1). The ratio of mean corolla lobe length to mean sepal length was not used in the generation of the nearest-neighbor tree.

## RESULTS

It appears that at least two distinct groupings of *Gonolobus* taxa exist in the southeastern United States. The clustering of taxa exhibits strong geographic tendencies (Fig. 1), although petal and sepal length intergrade among OTUs when graphed in a scatterplot (Fig. 2). Based on corolla coloration, taxa can be assigned to one of two groups: (1) a uniformly colored corolla group (UCCG) and a multi-colored corolla group (MCCG). The UCCG is considerably more widespread and exhibits a more western center of gravity relative to the MCCG (Fig. 1). Adaxial corolla pubescence is nearly invariable in the UCCG. Only 3.7% (3 of 81) of the examined individuals exhibit pubescent adaxial corolla surfaces (Fig. 3). Although individuals with uniformly colored petals have been collected in the far eastern states of Georgia, North Carolina, and Virginia, these tend to be rare collections disjunct from the main range of occurrence (Fig. 1).

TABLE 1. Floral characters and character states. Character 6 used in ANOVA only and not in generation of neighbor-joining tree due to lack of independence vis-à-vis characters 4 and 5.

Character	Character State	
1. Adaxial corolla coloration	Multi-colored (dark center, lighter tips) [0]	Uniformly green [1]
2. Adaxial corolla vestiture	Pubescent [0]	Glabrous [1]
3. Corona	Lobed [0]	Truncate [1]
4. Mean sepal length (mm)	1.5–2.5 [0], 2.51–3.5 [1], 3.51–4.5 [2], 4.51–5.5 [3]	
5. Mean corolla lobe length (mm)	2.01–4 [0], 4.01–6 [1], 6.01–8 [2], 8.01–10 [3], >10.01 [4]	
6. Ratio of Mean corolla lobe length: Mean sepal length	Continuous	

Adaxial corolla pubescence is much more frequent among members of the MCCG (Fig. 3). In fact, two thirds of the examined individuals in this group were pubescent (41 of 62). The MCCG appears to be restricted to a more narrowly defined southeastern range east of the Mississippi (Fig. 1).

Except for a few outliers (e.g., GA2, NC20, VA1, VA23), the geographic clustering is supported by the midpoint-rooted neighbor-joining tree (Fig. 4). Although bootstrapping yielded little support for any one branch of the tree (due to the small number of characters employed), the tree remains informative. Members of the MCCG and UCCG are grouped together—indicating greater within-group similarity across the five morphological characters than between groups.

Individuals of the UCCG exhibit longer mean corolla lobes (mean=7.68) and higher mean corolla lobe length to mean sepal length ratios (mean=2.48) than individuals of the MCCG (Table 2). Results of analyses of variation (ANOVA) indicate the differences in both mean corolla lobe length and corolla:sepal length ratio to be highly statistically significant between the two groups (Table 3).

It is interesting to note that the rare pubescent individuals of the predominantly glabrous UCCG appear to exhibit a similar frequency distribution of corolla lobe lengths and corolla:sepal ratios as pubescent members of the MCCG. ANOVA tests show no significant difference between pubescent UCCG and pubescent MCCG in both mean corolla lobe lengths ( $F=0.042 < F_{\text{Crit}}=3.99$ ) and the ratio ( $F=0.604 < F_{\text{Crit}}=3.99$ )—although this may be a factor of the small sampling size of pubescent UCCG members ( $n=3$ ). Glabrous members of the MCCG appear to exhibit corolla lobe lengths much larger than the more frequent (in terms of specimens examined) pubescent members of the MCCG (Fig. 5B). However, the difference in mean corolla lengths between glabrous and pubescent MCCG is not quite significant ( $F=3.559 < F_{\text{Crit}}=3.96$ ). The difference in the

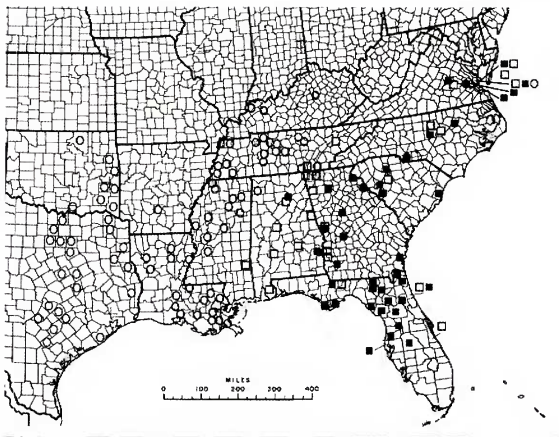


FIG. 1. Distribution map of southeastern United States *Gonolobus* entities. Circles represent individuals with uniformly green corollas—either glabrous adaxially (open circle) or pubescent (closed circle). Squares represent individuals with multi-colored corollas—either glabrous adaxially (open square) or pubescent (closed square).

corolla:sepal ratio between glabrous and pubescent MCGG members is also not quite significant ( $F=3.746 < F_{\text{Crit}}=3.96$ ). Although the frequency peak for corolla:sepal ratios of glabrous MCGG members appears to graphically coincide with the peak of glabrous UCCG members (Fig. 5C & D), ANOVA results show a strong statistical difference between the two ( $F=9.467 > F_{\text{Crit}}=3.93$ ).

#### DISCUSSION

The issue of whether more than one *Gonolobus* species should be recognized for the southeastern United States has long confronted taxonomists and has been additionally complicated by the nomenclatural confusion surrounding *Gonolobus suberosus* (L.) R.Br. (see Drapalik 1969; Reveal & Barrie 1992). Small (1933), and later Perry (1938), recognized two species of *Gonolobus* in the Southeast based on corolla pubescence and the ratio of corolla lobe length to sepal length. Small (1933) referred the taxon with glabrous corollas and lobes more than twice as long as the sepals to *G. gonocarpos* (*Vincetoxicum gonocarpos* sensu Small), whereas the taxon with pubescent corollas and lobes twice as long or less than the sepals was referred to *G. suberosus* (*V. suberosum* sensu Small).

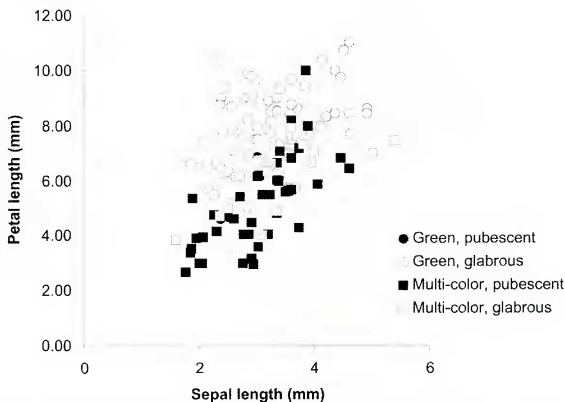


FIG. 2. Scatterplot of sepal vs. petal length by flower color and adaxial petal vestiture for *Gonolobus* entities in the southeastern United States.

Fernald (1950) added some less than distinct characters to the mix, including flower bud ("abruptly acuminate" vs. "gradually acute or acuminate"), calyx pubescence ("practically glabrous" vs. "glabrous or ciliolate apically"), and corolla lobe shape ("broadly lanceolate" vs. "linear-lanceolate"), while basically maintaining Small's (1933) pubescence and ratio characters. Gleason (1952) treated only *G. gonocarpus*, stating that *G. suberosus* was "erroneously" accredited to the range of Britton and Brown's flora. However, in a footnote, Gleason (1952) maintained the distinction between the taxa based on adaxial corolla pubescence, forwarded by previous authors (Small 1933; Perry 1938; Fernald 1950). In light of the present analyses, these concepts of specific delimitation are untenable as stated.

Drapalik's (1969) findings of overlapping combinations of character states among *Gonolobus* taxa in the southeast are upheld by our study. However, overlapping character presence/absence combinations are insufficient argument against recognition of multiple taxa. Especially at the infraspecific level and in hybrid zones, some level of character overlap can be expected between individuals sharing some range continuity. Our data support the notion of previous workers (e.g., Small 1933; Perry 1938; Fernald 1950; Gleason 1952), that at least two *Gonolobus* entities occur in the Southeast that could be accorded for-

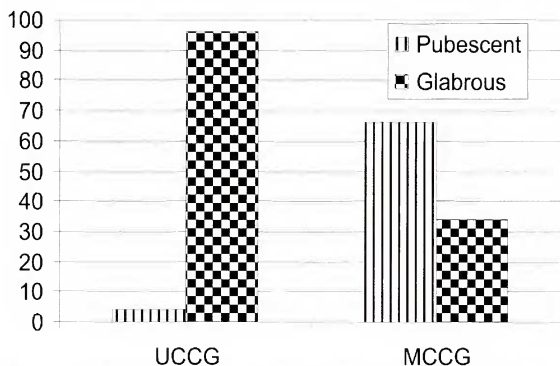


FIG. 3. Percentage of *Gonolobus* specimens exhibiting pubescent or glabrous adaxial corolla lobes in the respective uniformly colored corolla group (UCCG) and the multi-colored corolla group (MCCG).

mal rank. However, contrary to previous workers, we propose that the two groups respectively be defined by uniformly-green versus multi-colored corolla lobes, rather than by corolla/sepal length and adaxial corolla lobe pubescence. Although there are significant differences in mean corolla lobe lengths and the ratio of corolla lobe length to sepal length (Table 3), these character states can overlap at the individual level and cannot consistently separate the taxa. Similarly, adaxial corolla pubescence cannot consistently separate the taxa, being present in both members of the UCCG and the MCCG. However, distinct differences are apparent in the frequencies of the pubescence trait (Figs. 3 & 5). In addition, with respect to their geographic distribution, the frequency of glabrous, multi-colored flower collections increases conspicuously in the zones where the UCCG meets the MCCG (e.g., in Alabama). Similarly, the rare individuals bearing adaxially pubescent, uniformly green corollas occur well within the range of the MCCG. Thus, the respective changes in pubescence frequencies in the MCCG or occurrence of rare character states in the UCCG outside its primary range may be cautiously hypothesized to be an effect of genetic interchange between two taxa intergrading in distribution.

Unfortunately, frequency histograms of corolla lobe length and ratio of corolla lobe length:sepal length size classes within the UCCG and MCCG shed weak light on the matter of intergradation (Fig. 5). Although our analyses support the recognition of two *Gonolobus* entities in the Southeast, the question remains whether these should be recognized at the species level or below. Our



NJ

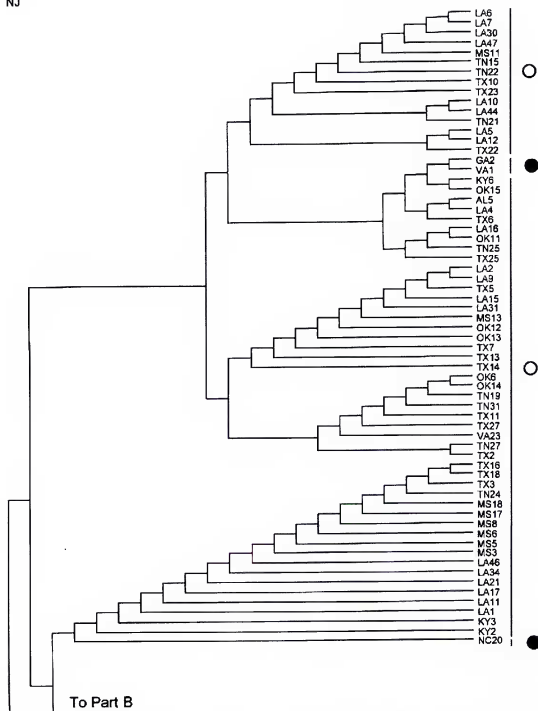


FIG. 4 (Part A). Midpoint-rooted neighbor-joining tree, based on five morphological characters. OTUs are individual specimens of *Gonolobus*. First two characters of alphanumeric code indicate state of origin by standard abbreviation. Second two characters are a unique, sequential number assigned to each specimen studied. Circles represent individuals with uniformly green corollas—either glabrous adaxially (open circle) or pubescent (closed circle). Squares represent individuals with multi-colored corollas—either glabrous adaxially (open square) or pubescent (closed square).

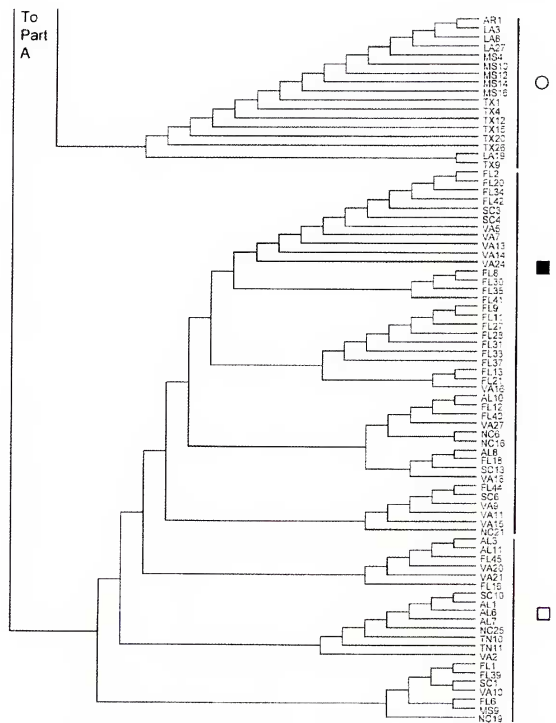


Fig. 4 (Part B).

data can be interpreted either way—two morphologically divergent species potentially hybridizing in overlapping zones, resulting in some morphological intergradation, or two diverging subspecies with morphological intergradation in zones of range overlap. The former interpretation could result from application of a quantitative or phenetic species concept, in which species are distinguished based on differences in means of variables. Although commonly

TABLE 2. Descriptive summary statistics for continuous floral characters of the uniformly colored corolla group (UCCG) and the multi-colored corolla group (MCCG).

	Mean sepal length	Mean corolla lobe length	Mean ratio (corolla lobe length: sepal length)
Uniformly colored	3.21 (SD=0.76)	7.68 (SD=1.47)	2.48 (SD=0.61)
Multi-colored	3.08 (SD=0.74)	5.59 (SD=1.73)	1.83 (SD=0.44)

TABLE 3. ANOVA results for floral character comparisons between the uniformly colored corolla group and the multi-colored corolla group. In both cases, the null hypothesis of no significant difference is rejected.

Source of Variation	SS	Mean corolla lobe length				
		df	MS	F	P-value	F crit
Between Groups	153.1516	1	153.1516	61.08722	1.15E-12	3.908255
Within Groups	353.5008	141	2.507098			
<b>Total</b>	506.6524	142				

Source of Variation	SS	Ratio of mean corolla lobe length: mean sepal length				
		df	MS	F	P-value	F crit
Between Groups	14.78613	1	14.78613	50.19068	6.1E-11	3.908255
Within Groups	41.53849	141	0.294599			
<b>Total</b>	56.32462	142				

applied, the underlying theory of this concept remains unclear (see Luckow 1995). In contrast, application of a phylogenetic species concept suggests two infraspecific taxa—populations exhibiting high frequencies of unique traits that may become ‘fixed’ in the future (Nixon & Wheeler 1990). However, a cladistic analysis that includes other congeners is necessary to test this hypothesis (Nixon & Wheeler 1990). In the absence of additional data, we cautiously choose to follow (Drapalik 1969) in recognizing a single species until additional evidence is available. Interestingly, the overall biogeographic pattern exhibited by the two *Gonolobus* entities has been observed for other taxa (including fish!) in the Southeast (see Avise 1994) and may be the result of past environmental shifts such as the oceanic incursions and retreats that define today’s southeastern Coastal Plain (Sorrie & Weakley 2001). To further elucidate both the question of rank and evolutionary history of the complex, we are conducting genetic analyses of southeastern *Gonolobus* populations using molecular markers and integrating phylogenetic data from Caribbean *Gonolobus* species—some of which have been suggested to be nearest relatives of the southeastern taxa (Scheele 1848).

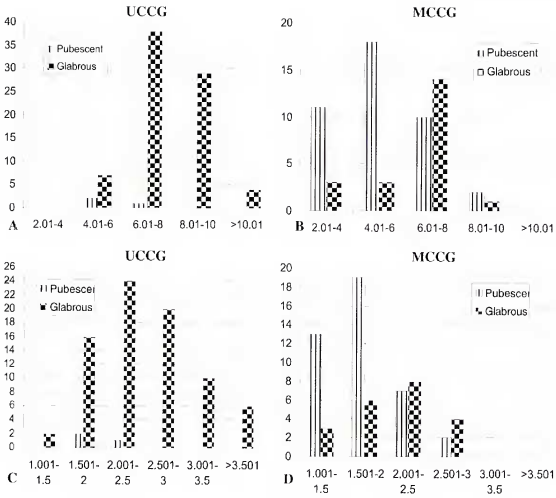


FIG. 5. Frequency histograms for floral characteristics in the uniformly colored corolla group (UCCG) and the multi-colored corolla group (MCCG) of southeastern *Gonolobus*—Corolla lobe length in mm ranges (A: UCCG; B: MCCG) and ratio of corolla lobe length to sepal length (C: UCCG; D: MCCG). Y axes represent number of individuals and X axes respective character state ranges.

Should workers choose to formally recognize the two entities, we provide a brief discussion regarding available names. For more detail regarding the particularly complicated history and nomenclature involved, readers are urged to see Reveal & Barrie (1992) and Krings (2001). In choosing a name for the taxon with uniformly colored petals, past names published for southeastern *Gonolobus* taxa were examined. Walter's type of *Gonolobus gonocarpus* (Walter 687, BM!) contains only leaves and roots. In addition, no mention regarding the pubescence of the corolla is made in his protologue (Walter 1788). Thus we cannot be certain to which species the plants that Walter based his description on belong. However, due to the rare occurrence of uniformly colored species in the Carolinas, we propose that his type be considered to belong to the multi-color group. Types for *Gonolobus macrophyllus* Michx. and *Gonolobus laevis* A. Gray, non Michx. are relegated to the multi-color group for the same reason. The

protologue of *Gonolobus granulatus* Scheele (1848) is based on the only eligible type specimen collected west of the Mississippi (*Lindheimer s.n.*) and notes glabrous adaxial corolla lobes. Thus, the correct name for the uniformly green-flowered taxon should be based on *Gonolobus granulatus* Scheele and the name for the multi-color flowered taxon should be *Gonolobus suberosus* (L.) R.Br. Alternatively, if the two entities are recognized at the infraspecific level, the correct species name is *Gonolobus suberosus* (L.) R.Br.

#### ACKNOWLEDGMENTS

We thank the following institutions and their curators for assistance with specimen inquiries, providing photographs of material, and/or providing specimen loans: BM, BRIT, DUKE, FLAS, GA, KY, LL, MISS, MO, NCU, NO, OK, P, TENN, TEX, UNA, USCH, USF, WILLI. Helpful methodological and nomenclatural comments were provided by Tom Wentworth and Paul Fantz, respectively. David Thomas provided PAUP support. Eric Sundell and an anonymous reviewer provided thoughtful comments on a previous version of the manuscript.

#### REFERENCES

- AVISE, J.C. 1994. Molecular markers, natural history, and evolution. Chapman and Hall, New York.
- DRAPALIK, D.J. 1969. A biosystematic study of the genus *Matelea* in the southeastern United States. Ph.D. Dissertation, University of North Carolina, Chapel Hill.
- EWAN, J. 1939. Bibliographical miscellany. III. Publication dates of Asa Gray's "Botanical Contributions." Amer. Midl. Naturalist 22:218–222.
- FERNALD, M.L. 1950. Gray's Manual of Botany. American Book Company, Boston.
- FORSTER, P.I. 1991. The correct publication dates for some genera and species of Asclepiadaceae described by Robert Brown. Asklepios 52:78–79.
- GLEASON, H.A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. New York Botanical Garden, Bronx.
- HOLMGREN, P.K., N.H. HOLMGREN, and L.C. BARNETT. 1990. Index Herbariorum. New York Botanical Garden, Bronx.
- KRINGS, A. 2001. Neotypification of *Enslenia albida* and a new name in *Ampelamus* for *Cynanchum laeve* (Apocynaceae, Asclepiadoideae). Sida 19:925–929.
- LIEDE, S. 1996. *Sarcostemma* (Asclepiadaceae) – a controversial generic circumscription reconsidered: Morphological evidence. Syst. Bot. 21:31–44.
- LIEDE, S. 1997. American *Cynanchum* (Asclepiadaceae)—A preliminary infrageneric classification. Novon 7:172–181.
- LIEDE, S. and A. TAUBER. 2000. *Sarcostemma* R.Br. (Apocynaceae—Asclepiadoideae)—a controversial generic circumscription reconsidered: evidence from trnL-F spacers. Plant Syst. Evol. 225:133–140.
- LUCKOW, M. 1995. Species concepts: assumptions, methods, and applications. Syst. Bot. 20:589–605.

- MABBERLEY, J. 1985. *Jupiter Botanicus—Robert Brown of the British Museum*. J. Cramer, Braunschweig.
- NIXON, K.C. and Q.D. WHEELER. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6:211–223.
- PERRY, M.L. 1938. *Gonolobus* within the Gray's manual range. *Rhodora* 40:281–287.
- RADFORD, A.E., H.E. AHLES, and C.R. BELL. 1968. *Manual of the vascular flora of the Carolinas*. University of North Carolina Press, Chapel Hill.
- REVEAL, J.L. and F.R. BARRIE. 1992. *Matelea suberosa* (L.) Shinnars (Asclepiadaceae)—once again. *Bartonia* 57:36–38.
- ROSATTI, T.J. 1989. The genera of suborder Apocynineae (*Apocynaceae* and *Asclepiadaceae*) in the southeastern United States. *J. Arnold Arbor.* 70:443–514.
- SCHEELE, A. 1848. Beiträge zur flor von Texas. *Linnaea* 21:747–768.
- SHINNERS, L.H. 1950. The species of *Matelea* (including *Gonolobus*) in North Central Texas (Asclepiadaceae). *Field & Lab.* 18:73–78.
- SHINNERS, L.H. 1964. Texas Asclepiadaceae other than *Asclepias*. *Sida* 1:358–367.
- SMALL, J.K. 1933. *Manual of the southeastern flora*. University of North Carolina Press, Chapel Hill.
- SORRIE, B.A. and A.S. WEAKLEY. 2001. Coastal Plain vascular plant endemics: Phytogeographic patterns. *Castanea* 66:50–82.
- STAFLEU, F.A. and R.S. COWAN. 1976. *Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types*, Vol. I: A–G. Bohn, Scheltema, and Holkema, Utrecht.
- STEARNS, W.T. 1960. An introduction to Robert Brown's "Prodromus florae novae hollandiae." Pp. V–LII in facsimile edition, Weinheim.
- STEVENS, W.D. 2001. Asclepiadaceae. *Monogr. Syst. Bot. Missouri Bot. Gard.* 85:234–270.
- SUNDELL, E. 1981. The New World species of *Cynanchum* L. subgenus *Mellichampia* (A. Gray ex S. Wats.) Woods. (Asclepiadaceae). *Evolutionary Monogr.* 5:1–62.
- SWOFFORD, D.L. 2002. PAUP 4.0b10. Sinauer Associates, Sunderland.
- WALTER, T. 1788. *Flora Caroliniana*. Murray Printing Co. (Photolithographers), Cambridge.
- WOODSON, R.E. 1941. The North American Asclepiadaceae. *Ann. Missouri Bot. Gard.* 28: 193–244.